THE TRACHEAL SYSTEM OF THE MATURE LARVA OF *PYRAUSTA NUBILALIS* HUBN.[1]

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The tracheal system of the larva of the European corn-borer, *Pyrausta nubilalis* Hubn. (Lepidoptera; Pyralididæ) is of the peripneustic type. There is one pair of functional spiracles on the thorax, and eight pairs on the abdomen. (Fig. 1). These spiracles open into short stout tracheæ which lead, on each side, to a large longitudinal trachea which runs throughout the length of the body, and from which branches go to the various body organs.

The Spiracles

The spiracles are of the type described by Kranchner, according to Packard (1909), as "bearing lips." The lips are represented by a chitinous ring surrounding the elliptical opening through the body wall. They are "roof-like," or bent inwards, and are hairy. (Fig. 2). From the spiracle a short stout trachea joins the adjacent longitudinal trunk. (Fig. 3).

The Tracheal Closing Apparatus

The tracheal closing apparatus (Fig. 3) surrounds the short trachea between the spiracle and the main trunk. On one side of the trachea, extending about half around it, is a chitinous band, the *closing bow*. Attached to one end of this bow is one extremity of the *closing lever*. The closing lever runs parallel with a line joining the ends of the closing bow, to a point almost halfway between the ends of the bow. Here the lever turns abruptly away from the

center of the trachea at approximately a right angle. The projecting arm thus formed is somewhat larger than the other arm and swells slightly toward its free end. The lever is chitinous. Between the apex of the lever and the end of the closing bow opposite to that to which the lever is attached is a third chitinous piece. This is the *closing band.*

The contraction of a muscle extending between the free arm of the lever and the closing band causes the lever to move. The attachment of the lever to the closing bow becomes the fulcrum, and the action of the muscle pulls the apex of the angle of the lever inward, causing the space between the lever and the closing bow to become constricted. The closing band is so attached to the apex of the angle that the end of the band is depressed inward, causing the space between it and the closing bow to be constricted. The trachea is thus pinched together.

This structure is cast with the exuvia when molting takes place.

Kranchner (1880), who first described the tracheal closing apparatus of insects, expresses the opinion that it originates as a local thickening of the tænidium.

The description of the spiracles and closing apparatus is taken from a former paper, (Crowell, 1926).

The Longitudinal Tracheæ

In the embryo the tracheal system arises as ectodermal invaginations which grow deeper, and from which branches are sent out. One running forward fuses with one running backward from the next anterior spiracle, and one running backward fuses with one running forward from the next posterior spiracle. Thus, longitudinal connections are formed between the spiracles, and these connections form the main longitudinal tracheæ. In the thorax there is a longitudinal system on each side dorsal to the main system. It is formed by the joining of dorsally running branches.

The longitudinal tracheæ lie on each side in an area between the small dorso-recti muscles and the great ventro-

recti muscles. In this area there are no longitudinal muscles, but it is crossed by sterno-tergal muscles.

Lying in front of all of the spiracles, except those in the prothorax, is a sterno-tergal muscle, and the longitudinal trachea except in the mesothorax and in front of the first abdominal spiracle, passes between these muscles and the body wall. In the prothorax the sterno-tergal muscle lies behind the spiracle. In the metathorax a large branch from the main trachea passes beneath this muscle. In the mesothorax the muscle is present and a trachea arising in a manner similar to the branch in the metathorax passes between it and the body wall. Thus in each body segment through which the main trachea runs it is held to the body wall by a muscle passing over it. (Fig. 4. The trachea is much longer in proportion to its thickness than here indicated).

According to De Guyse (1926) the primitive position of the spiracle located on the prothorax was in the membrane between the prothorax and mesothorax, and it has moved ahead to its present position. That would account for the fact that the sterno-tergal muscle lies behind the spiracle rather than in front of it, as in the abdomen.

DeGuyse (1926) explains the positions of the muscles in front of the first abdominal spiracle, and in the mesothorax, from a consideration of the larvæ of *Sthenopis* (Hepialidæ), as follows:

The thoracic spiracles are situated at a much lower level than those of the abdomen. In the abdomen the anterior lateral branch arising from the short spiracular trachea passes under the sterno-tergal muscle and anastomoses with the posterior lateral branch from the next preceding segment. The anterior lateral branch from the first abdominal spiracle passes as usual under the muscle, but since the second thoracic spiracle is at a much lower level, its posterior lateral branch fails to meet the anterior lateral branch from the abdomnial spiracle. The latter loses itself among the dorsal muscles. At the same time the lower visceral branch is found greatly enlarged, and anastomosed with a posterior branch of the first thoracic spiracle. The

second pair of spiracles thus loses its connection with the general respiratory system and ceases to function.

That means that the apparent branch in the metathorax, arising from the apparent main trachea and passing beneath the muscle, is, in fact, the main trachea, and the apparent main trachea is a branch. But it is hard to explain the tracheal branchings in the mesothorax on this basis.

The branch from the first abdominal spiracle passing forward beneath the sterno-tergal muscle, does not, in *Pyrausta nubilalis* "lose itself among the dorsal muscles," but becomes a part of the dorsal longitudinal system, sending branches to the metathoracic leg and to the wing-bud.

Figure 5 and figure 6 show the branches arising from the first and fourth abdominal spiracles, respectively. In the case of the branches arising from the first abdominal spiracle it is evident that the presence of the appendages of the metathorax, legs and wings, has made necessary more tracheal branches than are called for in the fourth segment where such appendages are absent.

But a study of the branches arising from the fourth abdominal spiracle fails to show any that takes over the role of the main trunk, if we consider that the branch from the first abdominal spiracle from which spring the tracheal supplies to the alimentary tract, the wing-bud, and leg, to be the anterior branch, or "main tracheal trunk" from that spiracle.

The apparent main tracheæ, the "lower visceral branch" of de Guyse, does not meet the posterior branch from the prothoracic spiracle until after it throws out branches in the mesothorax that are at least analogous with the branches from the first abdominal spiracle. (Fig. 7). It is rather difficult to see how these branches arose as secondary branches from the lower visceral branch from the first abdominal spiracle and the posterior branch from the prothoracic spiracle.

The Transverse Tracheæ

The longitudinal tracheæ of each side are connected by transverse tracheæ in every spiracle bearing segment, ex-

cept, possibly, the first abdominal. There is one in the mesothorax, although that segment does not bear a functional spiracle. There is one in the head.

The transverse trachea in the head lies in front of the supraœsophageal ganglion and just behind the body of the tentorium. The posterior arms of the tentorium pass above the trachea, close to its junctions with the main longitudinal tracheæ. This transverse trachea lies above the commissures between the supra- and subœsophageal ganglia. (Fig. 8).

Peterson (1912) describes and figures a cross trachea in the larva of the tomato-worm, *Protoparce carolina*, lying above the commisures between the supra- and sub-œsophageal ganglia, but in the tomato worm this trachea crosses the subœsophageal ganglion. In *Pyrausta nubilalis* it lies well in front of the ganglion. Peterson says nothing about the relation of this trachea to the tentorium, but from his figure, the trachea must lie well behind it.

The next cross trachea, which I have numbered 2-a, is a secondary branch. The primary branch from which it springs comes from the main trachea just after it leaves the prothoracic spiracle and its other branches will be described later.

Trachea 2-a runs on the outside of the muscle layer, and beneath the central nervous system.

In the prothorax there is a transverse system of tracheæ dorsal to the alimentary tract. These tracheæ are arranged in such a manner that I term the system the *diamond*. (Fig. 9).

A large branch arises from the thoracic spiracle. It runs forward a short distance, then branches into two good sized tracheæ, the larger being in front. Each of these branches meets a corresponding branch from the opposite side, and the double Y thus formed gives the shape that justifies my name for the arrangement. From the forward apex of the diamond branches go into the head. From the posterior apex a long branch goes backward and joins a branch from the main trunk that runs backward from the prothoracic spiracle Thus, counting each branch separately there are

three transverse connections crossing the ailmentary tract between the prothoracic spiracles.

Peterson (1912), in the tomato-worm, finds that in all cases except the transverse tracheæ described above, the cross tracheæ lie ventral to the nervous system. This is not always true in *Pyrausta nubilalis.*

Just behind the prothoracic spiracle there is a trachea, which I have numbered 1. This lies on the inner surface of the muscle layer. It crosses the nerve cord dorsally, terminating, usually, in the prothoracic ganglion. Near the base of the ganglion the trachea meets the corresponding trachea from the other side, and a cross connection, dorsal to the nervous system, and ventral to the alimentary tract, is formed (Fig. 10). Trachea 1 varies. It may be much reduced, forming only a very weak connection with the central nervous system, with the corresponding trachea of the opposite side entirely absent (Fig. 11). Sometimes the trachea to the ganglion is obviously from the left side, with the trachea from the right meeting it (Fig. 12), and sometimes the opposite is true. The branches from trachea 1 usually supply the muscles, but in one specimen a large branch ran to the nerve cord in front of the mesothoracic ganglion. (Fig. 13). In the figures the size of the tracheal connections with the ganglion is exaggerated.

Trachea 1 lies, apparently, at the junctions of the longitudinal muscles of the prothorax with those of the mesothorax, and is a useful landmark in locating the limits of these segments.

The next transverse trachea I have numbered 2 (Fig. 14). It lies in the mesothorax on the outer side of the muscle layer. It passes beneath the central nervous system just in front of the mesothoracic ganglion. In relation to the muscles and the nervous system and to tracheæ 1 and 3, which will be described next, it is, if not homologous to trachea 2-a, analogous to it.

Trachea 3 lies on the inner surface of the muscle layer and approximately marks the limits of the mesothorax behind and of the metathorax in front. It is a transverse trachea much as is trachea 1. A branch to the mesothoracic ganglion meets a branch from the opposite side, forming a

cross tracheal connection dorsal to the nervous system and ventral to the alimentary tract (Fig. 15).

Trachea 4 lies in the metathorax. It is on the outside surface of the muscle layer and crosses just in front of the metathoracic ganglion. It is similar to trachea 2.

The system of numbering is now evident. Beginning with the first trachea behind the prothoracic spiracle lying on the inside of the muscle layer, extending toward the mid-ventral line of the body, which trachea I have called 1, the tracheæ in each segment behind this that lie on the inner surface of the muscles at about the line between the segments have *uneven* numbers. Those transverse tracheæ lying in the segment and on the outer surface of the muscle layer have *even* numbers.

Trachea 5 is not a transverse trachea; and the tracheæ in the abdomen analogous to tracheæ 1, 3 and 5, are not transverse tracheæ.

Trachea 6 lies in the first abdominal segment. From its position on the outside of the muscles and from the distribution of its branches, which will be discussed later, it is analogous, if not homologous to the other tracheæ of like position (those with even numbers). But unlike tracheæ 2 and 4, and unlike the corresponding tracheæ in the abdominal segments, trachea 6 is not, as a rule, a transverse trachea. In one specimen I found a connection with the corresponding trachea from the opposite side. I doubt if that was typical. But it must be considered in connection with the transverse tracheæ because of its position. (Figs. 16, 17).

Behind the first abdominal segment there is a transverse tracheal connection in each spiracle bearing segment. From the second to the seventh segments inclusive, this transverse trachea is analogous to tracheæ 2 and 4, except that they lie behind, rather in front of, the ganglia.

In the eighth segment there is a stout connection between the spiracles lying above the alimentary tract.

Peterson (1912) in speaking of the tomato worm says: "In the case of the eighth abdominal segment, only one minute dorsal cross trachea was found, while in the prothoracic region two distinct cross tracheæ were observed."

Pyrausta nubilalis differs from the tomato worm in that the cross trachea in the eighth segment of the abdomen is not minute, but is a stout connection. In the prothorax the connections are apparently similar, but Peterson shows no tracheal connection between the posterior apex of the diamond and the main trunk.

Tracheæ from the Prothoracic Spiracle

The arrangement of the tracheæ from the prothoracic spiracle (Fig. 18), from which the organs of the prothorax and head are supplied, is much more complicated than that in the regions of the body behind the prothorax. It is easier to describe these tracheæ as from the prothoracic spiracle than to attempt to correlate them with the study of the tracheal supplies to various systems of organs.

From the spiracle two large branches extend towards the head. One of these I believe, for reasons to be set forth later, represents the main longitudinal trachea, or the anterior branch from the spiracle. The other branch forks a short distance in front of the spiracle, and its inner branch forms the stem of the Y which makes up one side of the dorsal transverse tracheæ to which I have referred as the diamond. The outer branch goes forward into the head. There it branches, and apparently supplies the great mandibular muscles lying in the side of the head. One branch was traced to the region of the base of the antenna, but I was unable to follow it into that organ.

The other large branch going into the head from the spiracle branches almost immediately. This first branch sends out a small branch, and three larger branches of about equal size. The small branch goes toward the head. The branch nearest the head of the other three branches passes at once to the outer surface of the muscle layer. It runs toward the middle of the body, and sends a branch to the prothoracic leg. It continues, and sends a branch upward to the prothoracic ganglion. Then it meets the corresponding trachea from the opposite side, forming a transverse connection ventral to the central nervous system. In its position and its branching to the ganglion, but not to

the leg, it resembles the transverse tracheæ to which I gave even numbers, and is the trachea which I designated as 2-a.

The middle of the three branches runs on the inner surface of the muscle layer and sends branches to the prothoracic and subœsophageal ganglia, and to the muscles.

The hindmost branch also runs on the inner surface of the muscle layer. It crosses the muscles, and bending ventrally sends a branch to the prothoracic leg.

The middle and hindmost branch, taken together, are, in their position and distribution so similar to trachea 3 that I believe them to be at least analogous to the tracheæ with uneven numbers. Therefore I have numbered them together as branches of trachea 1-a.

The next large branch from the main trachea runs largely across the dorsal surface of the muscles inside of the head, apparently supplying them.

A small branch runs from the main tracheal system to the supraœsophageal ganglion.

Just in front of this ganglion, and lying so that the main tracheal branch is just behind the body of the tentorium, is the first transverse trachea described above. There are two branches from this trachea extending backward. Sometimes they go to the subœsophageal ganglion (Fig. 18), and sometimes they end in the nerve cords anterior to it. In sending these branches to the nervous system, this trachea resembles tracheæ 2, 4, etc., but in lying above the neural commissures it differs from them.

In describing the main tracheæ from the spiracle I said that two large branches extend toward the head. From one springs the half of the dorsal transverse system forming the diamond. From the other spring branches 2-a, 1-a, the trachea to the supraœsophageal ganglion, and the first transverse connection, I believe that these branches indicate that this trachea is the main longitudinal trunk, and not the one giving rise to the diamond. For, as will be shown, the transverse tracheæ supplying the ganglia of the body segments posterior to the prothorax always spring directly from the main trunk near the spiracle. If it is true that the anterior arm of the tentorium is formed from an invagination of the body wall representing the spiracle

of the mandibular segment (Comstock and Kochi 1902), it is not unreasonable to imagine that the first transverse tracheæ indicate, at their point of origin, the positions of the branchings from a spiracle, and that it is here that the main longitudinal trachea ends, rather than at the prothoracic spiracle.

From just in front of the base of the transverse trachea two tracheæ of about equal size run forward. The inner one ends in two short branches, one to the maxilla, and one to the labium. The outer trachea sends branches into the mandible, and a branch to the region of the base of the antenna. I was unable to trace this into the antenna. A small branch from the trachea to the supraœsophageal ganglion runs forward and joins one of the mandibular branches.

The other tracheæ arising from the prothoracic spiracle are the posterior branch going into the formation of the main longitudinal trachea, and a branch also running backward which joins the trachea to the posterior apex of the diamond. Branches also go from this backward running branch to muscles and fat bodies, and a branch divides into tracheæ supplying the appendages of the mesothorax.

Tracheæ to the Nervous System

The tracheæ to the supra- and subœsophageal ganglia, and to the prothoracic ganglion have been described.

The mesothoracic ganglion is supplied with air by tracheæ 2 and 3. Trachea 2 sends a branch backward to the ganglion, and trachea 3 sends one forward as described.

Trachea 3 lies on the inner surface of the muscle layer and sends many branches to the muscles (Fig. 15). Its main branch runs around the edge of the muscle layer and, turning downward, extends into the mesothoracic leg.

Trachea 5 differs from trachea 1 and 3 in that it does not connect with the corresponding trachea from the opposite side. It sends branches to the muscles and its forward branch runs around the edge of the muscle layer, and turning downward, enters the metathoracic leg. It also

sends small branches to the metathoracic and first abdominal ganglia. (Fig. 19).

The metathoracic ganglion receives, in addition to the small branches from trachea 5, branches from trachea 4. These run backward, one on each side, to the ganglion. (See Fig. 14, representing trachea 2).

The first abdominal ganglion receives, on each side, a small branch running forward from trachea 6, as well as branches from trachea 5. (Figs. 16 and 17).

The abdominal ganglia receive their air supply from the transverse tracheæ. In the abdomen these all are found on the outside surface of the muscle layer. The tracheæ corresponding to tracheæ 1, 3, and 5, do not enter the nervous system. Another difference is that in the thorax the transverse tracheæ of even number, 2 and 4, lie in front of the ganglia and send their branches backward to them, while in the abdomen the transverse tracheæ lie behind the ganglia, and the branches to the ganglia run forward. The tracheæ that form the transverse tracheæ in the abdomen divide into an anterior and posterior branch. It is the posterior branch that meets the corresponding trachea from the other side, forming the transverse connection, and from this branch, also, that the branch divides that supplies the ganglion. The anterior branch may send branches to the ganglion, but apparently more often it does not. (Fig. 20).

The seventh and eighth abdomnial ganglia have coalesced and lie in the seventh abdominal segment. The trachea that normally would supply the seventh ganglion here supplies both. There is no separate connection between the eighth ganglion and the tracheal system. (Fig. 21).

Peterson (1912) figures two transverse tracheæ in the tomato-worm larva sending branches to these ganglia, the one supplying the seventh passing under the eighth, and the trachea sending branches to the eighth is apparently the transverse trachea between the spiracles of the eighth abdomnial segment. Careful search failed to discover any trachea from this transverse trachea to the nervous system in *Pyrausta nubilalis*.

The commissures between the ganglia are usually supplied by branches from the transverse tracheæ. In the ab-

domen there are branches between the branches to the ganglia, that run backward, usually one on each side of the mid-ventral line, and small branches from these sometimes enter the commissures. (Fig. 22). Lubbock, (1860) states that he found the commissures of adult Lepidoptera to be without tracheæ, but the commissures in the larvæ well supplied.

Occasionally the nerves from the ganglia have short tracheæ in them. This is more often the case at their origin, where a branch from the ganglion-supplying trachea often enters them (Fig. 23). Sometimes a small branch from the thoracic tracheæ, 3 and 5 will go to the nerve trunk (Fig. 24). In one specimen the anterior branch from the transverse trachea in the seventh abdominal segment sent a branch to a nerve originating in the seventh abdominal ganglion. (Fig. 25).

Tracheæ to the Appendages. (Fig. 26)

The tracheæ to the mandibles, maxillæ and labium have been described above. In the section describing the tracheæ from the prothoracic spiracle the courses of the tracheæ to the prothoracic leg were described. To briefly review:

The ventral trachea 2-a sends a branch to the leg; so does a branch of trachea 1-a. Both 1-a and 2-a spring from the same branch from the main trunk. The tracheal supply of the prothoracic leg, combined as it is with the supply to the nervous system, differs from that of the meso- and metathoracic legs, but resembles, somewhat the tracheal supply of the abdominal prolegs.

The mesothoracic leg receives its tracheæ from three sources. First a large branch from near the prothoracic spiracle runs backward. This sends a branch to the posterior apex of the diamond. Behind this branch, the trachea divides into a Y, the inner arm of which runs on the outer surface of the muscle layer toward the middle of the body, and forms the anterior stem of the leg tracheæ. The outer arm of the Y runs backward and joins, in the wing-bud, with a forward running branch of the next large outer branch of the main trachea. This large branch springs

from the main trunk behind, and on the opposite side to, trachea 3. It runs forward and its second branch is the outer arm of a Y which joins, in the wing-bud, the outer branch of the Y in the other trachea. The inner arm of this Y runs toward the center of the body, forming the posterior stem of the leg trachea, and anastomosing with the inner arm of the Y from the trachea arising near the prothoracic spiracle and the trachea formed by this union goes to the leg. Thus the mesothoracic leg is supplied by tracheæ from origins before and behind. Also, a branch of trachea 3 ends in the leg, making the supply from behind a double one.

The tracheæ to the metathoracic leg are similar to those to the mesothoracic leg. There is an anterior stem, arising from a branch from the main trunk, and a posterior stem arising from a forward directed branch of the main trunk. The branches of the main trunk also send branches out that meet in the wing-bud. These branches joining in the wing-buds of the meso- and metathoracic segments constitute the dorsal longitudinal trunk of the thorax. Trachea 5 sends a branch to the metathoracic leg in the same manner as does trachea 3 to the mesothoracic leg.

In the pupa of *Antheraæ pernyi* Guer., according to Enderlein, (1902), the arrangement of the tracheæ to the legs is very different from that of the larva of *Pyrausta nubilalis*. The prothoracic leg is supplied by two branches from the trachea to the antenna, and by two branches from a branch to the supraœsophageal ganglion, making four tracheæ enter this appendage. The meso- and metathoracic legs are each supplied by a single trunk.

Peterson (1912) figures the tracheal system of *Protoparce carolina* without showing the distribution of the branches, except in the case of the legs, and here he shows but a single trachea to each of them.

Chapman (in Comstock 1918) figures the tracheation to the meta- and mesothoracic legs in the pupa of *Antheræa roylei*, and his figure agrees, in the main, with the distribution shown by *Pyrausta nubilalis*. He does not show the supply to the prothoracic leg.

Regarding Enderlein's figure, Chapman says: "The con-

ditions of the tracheæ seem to be so constant in representatives of this order (Lepidoptera) which have been studied that it would seem very improbable that there should be such a great difference between two members of the same genus as Enderlein's figure would indicate."

Peterson's figure was drawn from a ventral dissection, and in the case of *Pyrausta nubilalis,* the tracheal supply to the prothoracic leg cannot be properly seen from this aspect, for the spreading of the insect breaks the transverse trachea 2-a, and the leg then appears to have either but one branch to it, or if two branches are seen to enter the leg, the transverse character of 2-a cannot be seen. With regard to the meso- and metathoracic legs, the least that can be said is that in the European corn borer their supply is very different from this supply as shown by Peterson in the tomato-worm.

The tracheal supply to the proleg of the third abdominal segment is shown in Figure 27. It is a branch running almost directly downward from, and at right angles to, the posterior branch of the trachea supplying the ganglion of the segment. The proleg trachea divides shortly after leaving the main branch, and two branches enter the leg. The anal proleg is supplied by a long branch running backward from near the eighth abdominal spiracle in a manner suggestive of the branch running forward, in the head, to the mandible. (Fig. 28).

The tracheal supply to the wing-buds has been described, and is apparent in the figure (Fig. 26).

Tracheæ to the Alimentary Tract, Fat Bodies, Silk Glands and Malpighian Tubules

The tracheæ to the alimentary tract, fat bodies, silk glands and Malpighian tubules must be treated largely under the same heading, for they are all branches from the same stems.

A large branch arises from the main tracheal trunk near its junction with the spiracular trachea. This branch runs across the body cavity and splits into branches, most of which supply the alimentary tract. These branches from

the main trunk are found arising from near the first to the eighth abdominal spiracles. None rise in the thorax.

Alimentary Tract

The trachea to the alimentary tract arising from near the first abdominal spiracle is different in origin from that observed in the other tracheæ supplying the tract. It does not arise directly from the main trachea, but is the first branch from the trachea that also gives rise to the posterior stem of the metathoracic leg tracheæ. The other tracheæ to the alimentary tract arise directly from the main longitudinal trunk.

The figure illustrating the tracheæ to the alimentary tract, (Fig. 29), shows the trachea arising near the first abdominal spiracle, and supplying that part of the tract just behind the œsophagus. In the figure this portion of the alimentary tract is shown much distended. As a rule the alimentary tract behind the œsophagus, from which it is distinctly separated, is of more or less uniform diameter throughout its length. This particular specimen is chosen for illustration, however, because the enlargement spreads the tracheæ, making their distribution easier to trace.

The supplying trachea arises as a branch of a trachea arising from the longitudinal trachea near to the spiracular trachea. The supplying trachea runs forward and upward, breaking into four main branches, one running forward and one running backward on the dorsal surface of the tract, and one running forward and one running backward on the ventral surface. These, with their branches, enclose the tract in a sort of basket of tracheæ.

This same arrangement appears in the tracheæ to the alimentary tract behind the first abdominal segment.

The œsophagus is poorly supplied with tracheæ. Sometimes a very small branch will enter it, but there is no basket-work of tracheæ around it, and no main tracheal branch to it.

Fat Bodies

The fat bodies are large masses of white material distributed within the body cavity somewhat as follows: A

mass on each side of the alimentary tract in the forward end of the thorax; a large mass which extends across the thorax below the alimentary tract, and which, therefore lies on both sides of the tract as well as beneath it; next come two large masses which largely fill the cavity of the abdomen; two masses, one on each side of the alimentary tract in about the seventh abdomnial segment; and a large mass in the caudal end of the body which lies on each side of the alimentary tract, and ventral to it. The large middle masses, one on each side, extend from about the first to the seventh abdominal segments; they are made up of large lobes, and each segment apparently has a lobe lying in it. No definite distribution of these bodies is made here with regard to the individual body segments, either in the thorax or abdomen, since they overlap each other. These are the large masses of fat that have been said to be storage of nutriment for metamorphosis, not the fat tissue about the body organs.

The first thoracic mass gets its air supply from the branch of the main trachea that also sends a branch to the apex of the diamond, a branch to the leg, and one to the wing-bud. Apparently the second thoracic fat body receives its trachea from the same source.

From the tracheal branches arising from the main longitudinal tracheal trunk near the spiracular tracheæ in the second to sixth abdominal segments, and which supply the alimentary tract, branches that supply the lobes of the largest fat body originate. The tracheæ from near the second and third spiracles apparently each supply a lobe of the fat body. The tracheæ arising near the fourth, fifth and sixth spiracles send branches into the lobes on each side of them, one forward, and one backward.

The supply to the fat lobe in the seventh segment is apparently a single branch from the trachea to the alimentary tract. The fat body in the eighth segment receives a branch from the tracheæ that run to the digestive system from each side of the body.

To reach the alimentary tract the tracheæ from the spiracles in the second to eighth segments cross the fat bodies dorsally.

Silk Glands

The tracheæ to the silk glands are small branches from the tracheæ supplying the fat bodies and alimentary tract. I only found them springing from the tracheæ in the second and third segments of the abdomen. (Fig. 30).

Malpighian Tubules

Two malpighian tabules on each side extend forward along each side of the alimentary tract from the caudal part of the body to opposite the fourth abdominal spiracle, where they turn and run backward. In the sixth, seventh and eighth abdominal segments, but mostly in the last two, the tubules become very convoluted and intertwine, and their individual characters are lost in the tangle.

Although carefully sought, no tracheal connections with the Malpighian tubules were found, except in the seventh abdominal segment. Here small branches arising from the trachea supplying the fat bodies and alimentary tract were traced to the walls of the Malpighian tubes. (Fig. 30). Figure 31 is a sketch of a branch broken from the supplying trachea to the alimentary tract which showed very plainly the small tracheal branches to a urinary tube.

Circulatory System

The circulatory system consists of a delicate tube in the dorsal part of the body. This is supplied by the ends of the large branches of tracheæ that also supply the dorsal muscles and the fat lying between them and the body wall. The tracheal endings in the circulatory organ are very fine, not numerous, and somewhat difficult to see.

Near the eighth abdominal spiracle several of the branches break up into a great number of very fine tracheæ (Fig. 32). These fine tracheæ lie in, or on, a membrane. They are not connected with the alimentary tract, except incidentally, for removal of the tract leaves most of them undisturbed. Such structures do not occur in the branchings from any other spiracle. That they have anything

to do with the circulatory system is a question. But on the suggestion of Prof. C. T. Brues that they may aerate the blood, I tentatively place them in the group of tracheæ to the circulatory system.

Reproductive System

The gonads are two whitish kidney-shaped bodies lying on each side, adjacent to the heart, in the fifth abdominal segment. They resemble, somewhat, the adipose tissue in which they are imbedded.

In the fifth abdominal segment the tracheæ, which in the other abdominal segments supply the dorsal muscles, the heart, etc., send two branches to the reproductive organs. There is a branch to the muscles, etc., then a branch to the gonad, another branch to the muscles, etc., followed by another branch to the gonad, and another branch to the muscles, etc. It is a fan-like arrangement, with the first, third, and fifth branches to the muscles, fat tissue and circulatory organ, and the second and fourth branches to the gonads.

The tracheæ to the gonads divide into several branches, just as they reach the organs, and branches are sent to various parts of the reproductive organs. (Fig. 33).

Tracheæ of the Muscles

The muscles lying between the longitudinal tracheæ and the mid ventral line receive their air from branches from the transverse tracheæ, and also from those tracheæ of uneven number that lie adjacent to the origin and insertion of the muscles at the edges of the segments.

The muscles lying between the longitudinal tracheæ and the heart receive the principal branches of those branches that end in the heart.

Figures 14 and 15 show the distribution of tracheæ 2 and 3 with their branches to the muscles and illustrate the muscular supply.

Fat Tissue

The fat tissue surrounding the organs, not the fat bodies, receives its air supply from small branches of the tracheæ to the organs. Figure 22 shows tracheæ to fat tissue about the central nervous system.

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Literature Cited

Chapman, R. N. The Basal Connections of the Tracheæ of the Wings of Insects. In Comstock, J. H., "The Wings of Insects," pp. 27-51, figs., 17-35. Ithaca, 1918.

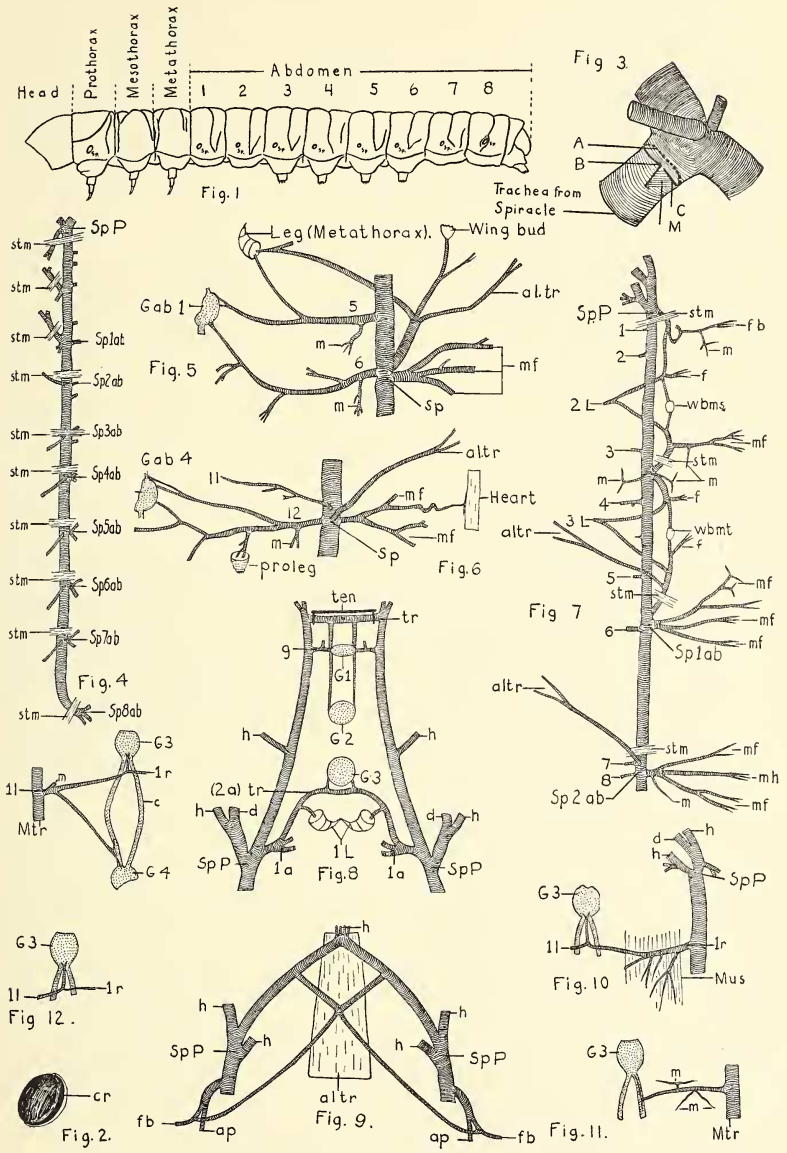
Comstock, J. H. and Kochi, C. The Skelton of the Head of Insects. American Nat. Vol. 36, pp. 13-45. 29 fig. 1902.

Crowell, M. F. The European Corn Borer: The Relation of the Larvæ to Submergence. New Hampshire Agr. Exp. Sta. Tech. Bul. 30. pp. 1-19. 7 fig. 1926.

De Guyse, J. J. The Morphogeny of Certain Types of Respiratory Systems in Insect Larvæ. Trans. Roy. Soc. Canada, Third Series, Vol. XX, Sec. V., pp. 483-503, 3 pl. 1926.

Enderlein, G. Eine einseitige Hemmungsbildung bei Telea polyphemus von ontogenetischen Standkpunkt. Zool. Jahrb., Anat. XVI, pp. 571-614, pls. 40-43. 1902.

Kranchner, O. Der Bau der Stigmen bei den Insekten. Zool, Anzeiger, p. 587. 1880.



Crowell-Tracheal System of *Pyrausta nubilialis.*

Lubbock, J. On the Distribution of the Tracheæ in Insects. Trans. Linn. Soc. Vol. XXIII, pp. 23-50, 4 pl. 1860.

Packard, A. S. A Text-Book of Entomology. 1909.

Peterson, A. The Anatomy of the Tomato-Worm Larva, *Protoparce carolina*. Ann. Ent. Soc. America, Vol. 5, pp. 246-268, pl. XIX-XXI. 1912.

Description of Plates

Plate I

Fig. 1. Sketch showing positions of spiracles.

Fig. 2. Prothoracic spiracles viewed so that interior can be seen.

Fig. 3. Trachea from spiracle with tracheal closing apparatus.

Fig. 4. Main longitudinal trachea showing positions of sterno-tergal muscles.

Fig. 5. Tracheæ arising from first abdominal spiracle.

Fig. 6. Tracheæ arising from fourth abdominal spiracle.

Fig. 7. Distribution of tracheæ between prothoracic and second abdominal spiracles.

Fig. 8. Transverse trachea in head, and ventral transverse trachea in prothorax.

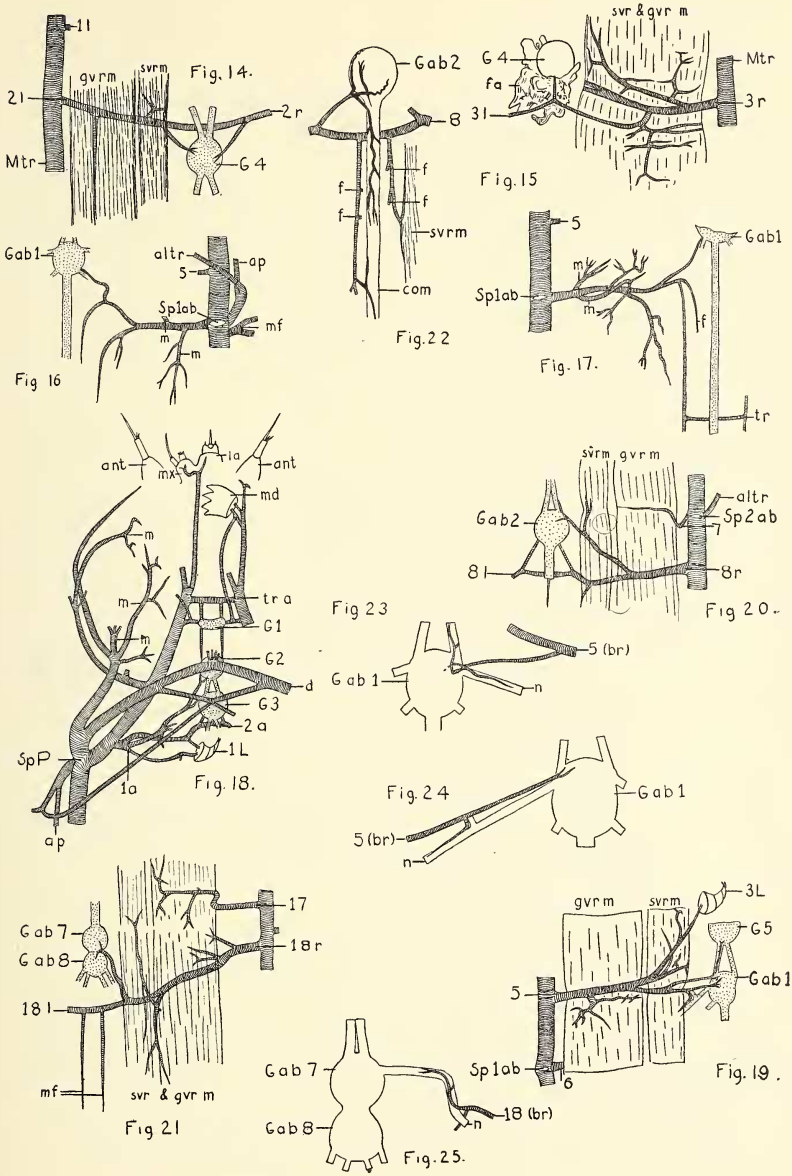
Fig. 9. Dorsal transverse tracheæ between prothoracic spiracles: The Diamond.

Figs. 10, 11, 12, 13. Trachea 1, and some of its variations.

Plate II

Fig. 14. Transverse trachea 2.

Fig. 15. Trachea 3, showing relation to ganglion and muscles.



Crowell-Tracheal System of *Pyrausta nubilialis.*

Fig. 16. Trachea 6.

Fig. 17. Trachea 6, showing a transverse connection.

Fig. 18. Tracheæ arising from prothoracic spiracle.

Fig. 19. Trachea 5.

Fig. 20. Tracheal supply to second abdominal ganglion.

Fig. 21. Tracheæ to seventh and eighth abdominal ganglion.

Fig. 22. Tracheæ to neural commissures.

Figs. 23, 24, 25. Tracheal supply to nerves.

Plate III

Fig. 26. Tracheæ to thoracic appendages.

Fig. 27. Trachea to proleg of third abdominal segment.

Fig. 28. Trachea to anal proleg.

Fig. 29. Trachea to alimentary tract.

Fig. 30. Tracheæ to fat bodies, silk gland, and Malpighian tubules.

Fig. 31. Detail of tracheal supply to a Malpighian tubule.

Fig. 32. Showing fine tracheæ, arising near eighth abdominal spiracle, and placed tentatively with tracheæ to circulatory system.

Fig. 33. Tracheæ to the gonads.

Abbreviations Used on Figures

A. closing bow of tracheal closing apparatus.

a. fat body in posterior part of thorax or in first abdominal segment.

altr. alimentary tract, or tracheæ to alimentary tract.

ant. antenna.

ap. tracheæ to appendages.

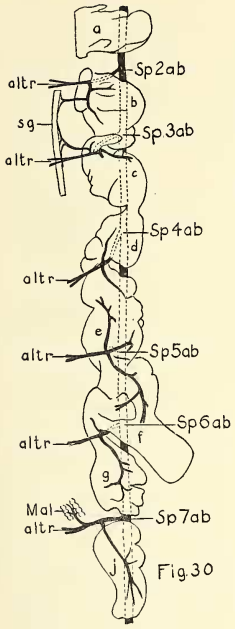


Fig. 30

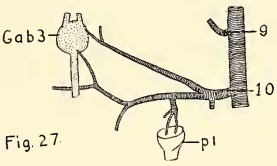


Fig. 27.

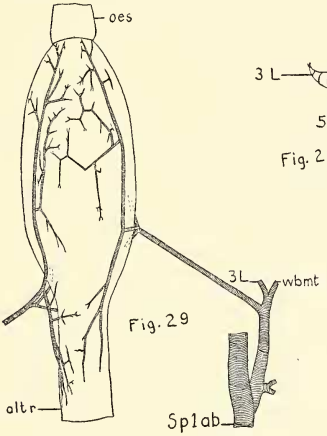


Fig. 29

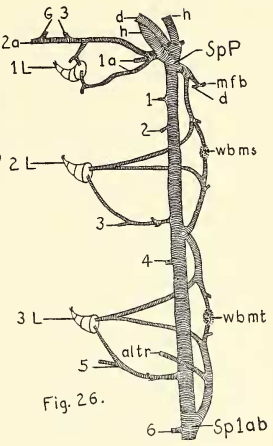


Fig. 26.

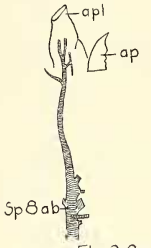


Fig. 28.

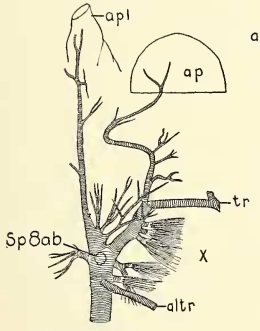


Fig. 32

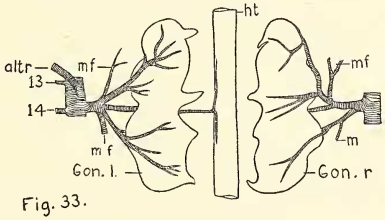


Fig. 33.

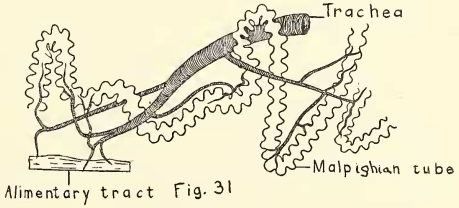


Fig. 31

Crowell-Tracheal System of *Pyrausta nubilalis*.

ap. (Figs. 28 and 32) anal plate.

apl. anal proleg.

1a, 2a. Tracheæ 1a and 2a.

B. Closing lever of tracheal closing apparatus.

(br.) Branch. (Number preceding indicates from which trachea.)

bg. (Fig. 30). Large fat body in 2nd to 7th abdominal segments.

C. Closing band of tracheal closing apparatus.
c. neural commisure.

com. commissure.

cr. chitinous ring.

d. trachea to diamond.

f. tracheæ to fat tissue.

fa. fat tissue.

fb. tracheæ to fat bodies.

g. trachea to supraœsophageal ganglion.

G1. supraœsophageal ganglion.

G2. subœsophageal ganglion.

G3. prothoracic ganglion.

G4. mesothoracic ganglion.

G5. metathoracic ganglion.

Gab. abdominal ganglion. Number attached indicates abdominal segment to which ganglion belongs.

Gon. gonad (l) left; (r) right.

gvrm. great ventro-recti muscle.

h. trachea to head.

ht. heart.

j. fat body in 7th abdominal segment.

L. leg, or trachea to leg; 1, prothoracic, 2, mesothoracic, 3, metathoracic.

la. labium.

M. muscle of tracheal closing apparatus.

m. tracheæ to muscles.

Mal. Malpighian tubule.

md. mandible.
mf. tracheæ to muscles and fat tissue.
mfb. tracheæ to muscles and fat body.
mh. tracheæ to muscles and heart.
Mtr. main longitudinal trachea.
Mus. muscle layer.
mx. maxilla.
n. nerve.
oes. œsophagus.
pl. proleg.
Sp. Position of spiracle. SpP., prothoracic, Sp. 1 ab. to Sp. 8 ab., abdominal spiracles. Numbers indicate segments.
Strm. Sterno tergal muscle.
svrm. small ventro-recti muscle.
ten. tentovium.
tr. transverse trachea.
wbms. mesothoracic wing-bud.
wbmt. metathoracic wing-bud.
1-18. Tracheæ of such numbers.